

## CAINOZOIC TURTLES FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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The Chelidae and Meiolaniidae occur in the Oligo-Miocene at Riversleigh with the former dominant and short-necked *Elseya/Emydura* accounting for over 90% of turtle material. *Chelodina* and *Pseudemydura* are present with several undescribed forms. Chelid diversity increased from the Oligocene to the Miocene, while average size decreased, suggesting a change in the aquatic habitats. I propose that large late Oligocene river and overflow systems were replaced by smaller, slower-flowing waterways that by the mid-Miocene had developed numerous small, stationary aquatic habitats, some occupied by dwarf turtles.

The Miocene appearance and radiation of the large terrestrial meiolaniid turtles and their presumed thermal and dietary requirements suggest that Riversleigh's gallery forests were heterogeneous and punctuated by open clearings. Absence of trionychid turtles and death of long-necked chelids may be related to the general unsuitability of habitats at Riversleigh, particularly during the Oligocene. □ *Australia, Riversleigh, turtles, palaeoecology.*

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Riversleigh's Oligocene and Miocene turtles (White, 1988, 1990, 1992; Gaffney et al., 1989; White & Archer, 1989) represent the highly aquatic side-necked Chelidae and the large, terrestrial, horned Meiolaniidae.

Chelid remains are common in Systems A, B and C of Archer et al. (1989, 1994) and are known from Pleistocene gravels (Terrace Site) adjacent to the Gregory River (White & Archer, 1994). Living specimens of the presumed extinct *Elseya lavarackorum*, have been collected from nearby Lawn Hill Creek and subfossil material from near the Gregory River (Thomson et al., 1997). Meiolanid remains are confined to System B and one site in System C (Gaffney et al., 1992).

Riversleigh turtle material including skulls is well preserved (White & Archer, 1993) but no articulated remains have been found. Relationships of extant chelids have been based almost exclusively on cranial anatomy (Gaffney, 1977, 1979) but biochemical techniques are establishing alternative phylogenies (Georges & Adams, 1992) and derived shell features have been used to define fossil species (White & Archer, 1994).

### FAMILY CHELIDAE

The extant chelids *Pseudemydura*, *Emydura/Elseya* and *Chelodina* have been reported from the Oligocene-Miocene of Riversleigh (White, 1988; Gaffney et al., 1989; White & Archer, 1989).

Chelid taxonomy is based heavily on features of the skull (Gaffney, 1977, 1979). There are no derived skull characters known that can be used to distinguish *Emydura/Elseya* despite these genera being electrophoretically distinct (Georges & Adams, 1992). Shell features are not normally used because they have been presumed to be variable in chelid lineages (Gaffney, 1977) but some diagnostic shell features are now known (White & Archer, 1994; Thomson & Georges, 1996). I adopt the more conservative position of using skull features to distinguish short-necked chelids. Gaffney et al. (1989) reported on *Emydura/Elseya* skull material from Riversleigh although shells and shell pieces were available. Scute features are used to identify modern taxa but these have little or no phylogenetic value (Gaffney, 1979).

Riversleigh Oligocene-Miocene turtles are dominated, both in abundance and diversity, by short-necked chelids of which *Emydura/Elseya* were most common (White & Archer, 1989), representing over 90% of identifiable material, and are known from 10 fossil sites. These two genera contain nearly 60% of extant chelid species (Georges & Adams, 1992). Two mandibular pieces from Riversleigh's Bob's Boulders (System C) are the only remains assignable directly to *Elseya*. They have alveolar ridges typical of the *Elseya dentata* species complex.

A single skull fragment and partial plastron of *Pseudemydura* is known from Ringtail Site (System C; Gaffney et al., 1989). This genus contains

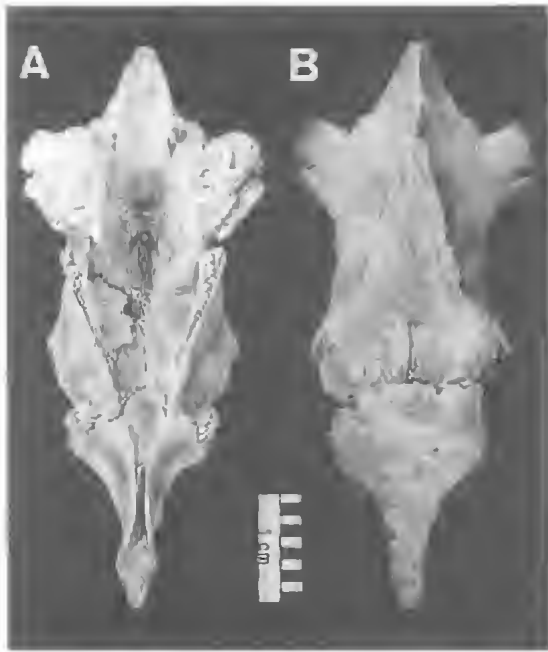


FIG. 1. Skull of *Chelodina* sp., QMF31303, Quentin's Quarry, Riversleigh. A, dorsal. B, ventral.

a single extant species, the Western Swamp Tortoise (*P. unbrina*), an endangered species confined to two small swamps north of Perth (Cogger, 1992). The Riversleigh specimen is the first fossil record of the genus and indicates *Pseudemydura* was once much more widespread. *Pseudemydura* is the most derived extant chelid (Gaffney, 1977, 1979) and is unusual among pleurodires in having little temporal or posterior emargination of the skull. This results in a skull with a near complete roof above the cranium. The Riversleigh skull fragment consists of a massively expanded supraoccipital indicating that enclosure of the hindmost portion of the skull occurred before the Miocene. Similarity of the Riversleigh specimen to the modern species suggests that *Pseudemydura* diverged from other short-necked chelids early in the Australian radiation, a conclusion supported by cladistic analysis of modern chelid skull features (Gaffney, 1977). Electrophoretic data (Georges & Adams, 1992) did not include *Pseudemydura* and Gaffney's (1977) hypothesis that *Pseudemydura* is the sister-group to all other Australian chelids remains (but see Manning & Kolfron, 1996).

Long-necked chelids arose before the Oligocene (Manning & Kolfron, 1996). Georges & Adams's (1992) indicate that *Chelodina* is the sister group to all Australian short-necked turtles

(excluding *Pseudemydura*). An almost complete plastron and some carapace bones of a small long-necked *Chelodina* are known (Gaffney et al., 1989). A species of *Chelodina* from Quentin's Quarry Site is described below. An almost entire carapace of a diminutive chelid from Melody's Maze Site (System C) and a partial skull from CMP Site (System C) White (1992, 1993) are described below.

#### SYSTEMATICS

Order TESTUDINES Linnaeus, 1758  
 Infraorder PLEURODIRA Cope, 1863  
 Family CHELIDAE Gray, 1825  
 Subfamily CHELINAE Gray, 1825

#### *Chelodina* sp. (Fig. 1)

MATERIAL. QMF31303, dorsal skull elements consisting of a fused frontal, paired parietals and prootics and supraoccipital bones from Quentin's Quarry Site, middle Miocene, System C.

DESCRIPTION. Frontal fused, detached from parietals, with suture undamaged. Posterior tip of supraoccipital missing. Parietals joined, sutured to their respective prootics and the supraoccipital. Frontal flat, roughly triangular, with maximum width behind rim of the orbit near the suture for the postorbital bones, with long and tapered anterior aspect, with the suture for the prefrontal as well as the rim of the orbit. Suture with the parietals horizontal. Parietals wider than frontal at their suture, widest in the posterior section of the orbit near their sutures with the postorbital bones, with dorsal aspect drawn into a tapering sagittal crest terminating with the intrusion of the supraoccipital to form the very tip of the crest. Supraoccipital forming roof of the posterior cranium; parietals forming roof for the majority of the vault. Cranium widest near the parietal-prootic suture. Prootics large, inflated, with suture attachments for the quadrate and basisphenoid intact, with latter suture uniting a broad foot-like plate of the quadrate with the basisphenoid.

DISCUSSION. This specimen is referred to *Chelodina* on the basis of the fusion of the frontal bones, absence of temporal skull roofing and lack of contact between the parietals and squamosals (Gaffney, 1977). Goode (1966) and Legler (1985) divided *Chelodina* into: the *C. longicollis* group (A) containing *C. longicollis*, *C. steindachneri* and *C. novaeguinea* and the *C.*

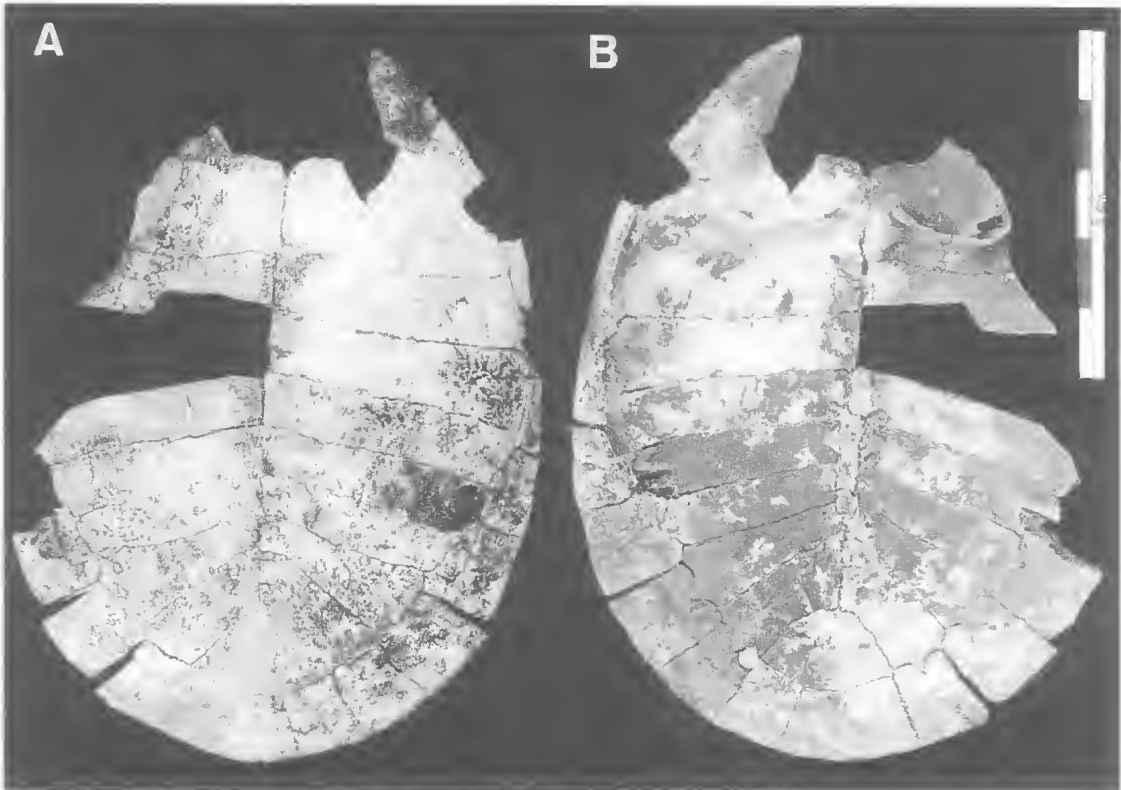


FIG. 2. Carapace of small turtle, QMF31304, Melody's Maze, Riversleigh. A, dorsal. B, ventral.

*expansa* group (B) containing *C. expansa*, *C. rugosa*, *C. oblonga* and *C. parkeri*. Goode (1966) separated short-necked species (Group A) where neck length is less than shell length, the posterior skull is not disproportionately extended, the basioecipital is large and expanded anteriorly, while the squamosal is reduced and lacks a protruding lateral process. Group B long-necked turtles were longer-necked where neck length is often longer than shell length, the posterior skull is markedly elongated, the basioecipital is small and squarish, and the squamosal has a prominent lateral process. Electrophoretic data (Georges & Adams, 1992) support these groupings but not their generic status. In particular, they disagree with the placement of *C. oblonga* and its relationship to the *C. longicollis* group.

The Quentin's Quarry shell cannot be readily allocated to either group although the skull shows no marked posterior elongation. The skull is unique in: 1. Contribution of the frontal bone to the orbit. In living *Chelodina* frontals are fused, forming a flat, dorsal plate behind the orbit with a thin medial process extending to the nasal re-

gion. The anterior process is intimately fused to the prefrontals which make up most of the dorsal orbit. The Quentin's Quarry skull has a thin medial process but the suture points with the prefrontals are minimal and anterior. The frontal process bears the rim of the orbit behind the prefrontal sutures and makes up the majority of the dorsal orbit. This means that the eyes were relatively closer together and directed more upwards than sideways. 2. Expanded anterior parietals. In modern long-necked turtles the anterior parietals are flat dorsally but curve steeply down to form the walls of the anterior cranium. In the Riversleigh specimen, there is a parietal shelf formed by the extension of the parietals. The postorbital bones are fused to this shelf which forms part of the roof of the post-orbital canal). 3. Triangular sagittal crest. In extant long-necked turtles the parietals are flattened dorsally before being drawn into a narrow, elongate mid-cranial crest that extends to the rear of the skull. This leaves a massive canal for the neck and jaw musculature. In the Quentin's Quarry skull, the dorsal parietals taper evenly to the back of the skull creating the most

robust crest of any known *Chelodina*. 4. Enlarged prootic bones. In modern *Chelodina* the prootics are fused laterally to the parietals. As such, they form a horizontal beam connecting the cranium to the external ear. In the Quentin's Quarry specimen the prootics are inflated producing a gradual sloping from the side of the skull down to the quadrate. The temporal canal is therefore triangular in profile with the majority of the canal space being more lateral and closer to the quadrate. 5. Restricted posterior extension of the skull. All modern long-necked turtles have low, elongate skulls. This is achieved by the extension of the mid and hind skull regions in the horizontal plane. In particular, the supraoccipital, quadrates, squamosals and opisthotics are markedly elongated. The Quentin's Quarry skull has an almost rectangular supraoccipital that would scarcely have extended beyond the external ear. 6. Shape of cranial vault. In modern *Chelodina* the cranium is widest near the frontal-parietal suture. In the Riversleigh long-necked turtle, the vault is widest in the mid-parietal, close to the prootic contact zone.

Genus indet. A  
(Figs 2, 3)

**MATERIAL.** QMF31304, an almost entire carapace and right femur from Melody's Maze, Gag Plateau, Riversleigh, System C, middle Miocene (Archer et al., 1989).

**DESCRIPTION.** Carapace elongate, oval, 100mm long, 75mm wide across pleurals 4. Shell without keeling along the midline, lacking serrated posterior peripherals, relatively low and flat in profile, with a longitudinal vertebral depression running the length of the shell, without fenestra. Pygal without division or indentation. Pleurals 11, relatively small. Peripherals increasing in size towards the posterior, with peripherals 8 and 9 the largest; peripherals 3, 4 and 5 and part of 6 curved ventrally, forming rounded shell margin associated with the bridge; anterior and posterior to the bridge, peripherals flattened, forming lateral platforms around the shell. On the inside of the carapace, rib heads on each of the pleurals. Pelvic scars well-developed on pleurals 8 and the suprapygal bones. Transverse ridge running across the floor of pleural 1 from the raised rib head to the recess for the bridge. Recess curved anteriorly, meeting the peripherals near the suture between peripherals 2 and 3.

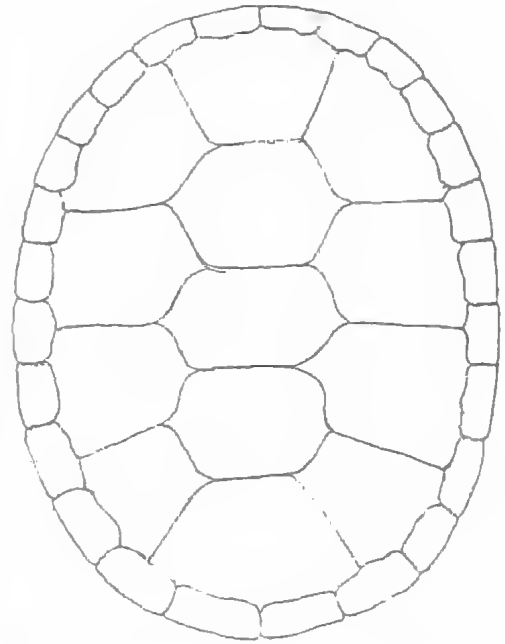


FIG. 3. Scute boundaries (dorsal) of QMF31304, turtle carapace from Melody's Maze.

**DISCUSSION.** The carapace has almost all of the right side intact, lacking only the third peripheral and nuchal bones. The left side is damaged and lacks peripherals 1 to 7 and portions of pleurals 1, 2 and 3.

The Melody's Maze carapace may be tentatively assigned to *Emydura* on the curved bridge recess and raised transverse ridge running across the floor of the first pleural bone (White & Archer, 1994). However, the pelvic scars on pleurals 8 and the suprapygals are more typical of *Elseya*. The shell is very small although it is from an adult animal. Its adult features include the closure of the carapacial fenestral, the tight fusion of the peripherals to the pleurals and the absence of features such as keeling of the carapace and expansion and flaring of the peripherals. The shell shows signs of advanced age: the extended growth of the pleurals during adult life has created a vertebral groove running the length of the carapace.

This shell cannot be placed in any of the known species of *Emydura* because of its small adult size and the unusual formation of the mid-peripheral bones. Among extant *Emydura*, the smallest known adults are in *E. signata* (Cogger, 1992) from the coastal rivers of northern NSW. Adult *E. signata* from the MacLean River show similar

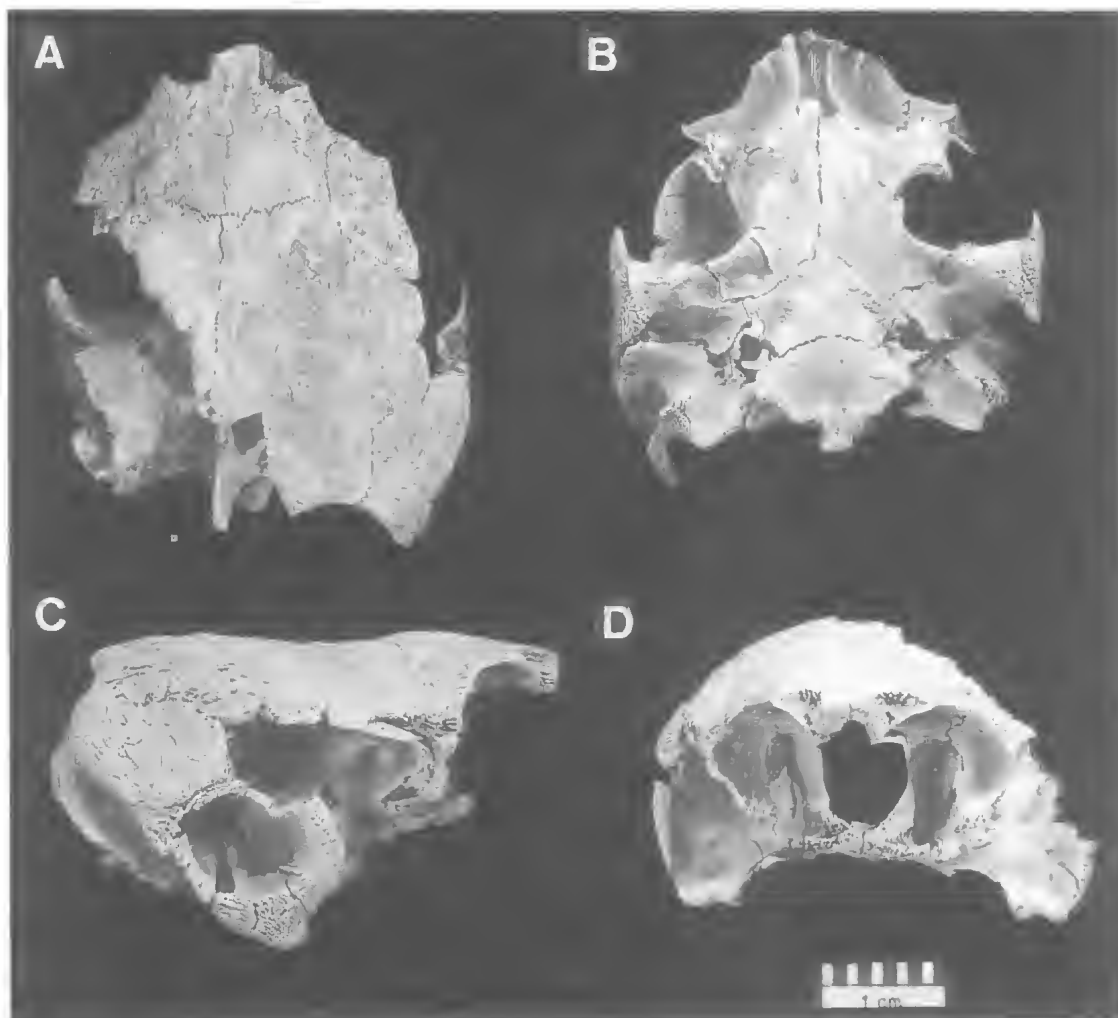


FIG. 4. Turtle skull, QMF31305, CMP Site, Riversleigh. A, dorsal. B, ventral. C, right lateral. D, posterior.

features to those of the Melody's Maze shell with carapace lengths of approximately 150mm.

Curving of the mid-peripheral bones associated with the bridge occurs elsewhere only in *Elseya dentata*-like turtles. In modern short-necked turtles, the peripherals are flattened and project laterally to form distinct ledges around the shell margin. The posterior peripherals are often flared to produce 'wings' that cover the hind limbs. There is virtually no flaring of the peripherals in the Melody's Maze shell; the peripherals are small compared to the pleurals (an adult growth trend in all chelids exaggerated in this species). Peripherals make up only 14% of the dorsal surface of the mid-carapace whereas *Emydura* (e.g., *E. krefftii*) the peripherals account for 20%.

The flattened shell is unlike most *Emydura* species which have domed shells. Only in *Pseudemydura*, *Chelodina*, *Elseya latisternum*-like turtles and some *Elseya dentata*-like species are the shells flattened and the central crest lost.

**Genus indet. B**  
(Fig. 4)

**MATERIAL.** QMF31305, a partial skull comprising the paired frontals, parietals, post-orbitals, quadrates, right squamosals and supraoccipital, with paired pterygoids, quadrates, prootic bones, opisthotic bones, exoccipitals, basisphenoid and basioccipital from CMP Site, Gag Plateau, Riversleigh, middle Miocene, System C.



**DESCRIPTION.** Medium-sized, with extensive dorsal roofing, lacking temporal and posterior emarginations that typify most chelids (Gaffney, 1979a). Parietals expanded, forming the bulk of the dorsal roof; squamosals broad, forming the temporal bridge; supraoccipitals only contributing to the mid-dorsal section of the skull roof, weakly expanded in the dorsal plane.

Frontals paired, with small, anterior, medial projections dividing the prefrontals, contributing minimally to the hind orbit. Postorbitals mainly in the dorsal plane, with a descending strut forming the posterior wall of the orbit. Sutures for the jugal evident. The descending strut from the postorbital and ascending process from the pterygoid in broad contact. Alary process of the pterygoid reduced, may not descend ventrally below the level of the palate. Postorbital canal correspondingly more obvious in lateral view.

Dorsal skull sloping downwards anteriorly. Squamosal broad, forming a broad temporal arch between the quadrate and the parietals. Quadrate large, with a deep angular ventral base continuous with the articulation facet for the lower jaw. Quadrate with a deep posterior vertical groove.

Floor of the skull widening markedly where the parietals sweep laterally to unite with the quadrates. Articulation facet for the lower jaw well below the level of the palate, with a broad area formed by the lateral extension of the pterygoid and the quadrates. Pterygoids with a transverse suture with the palatines. Basisphenoid triangular, with a broad sutural contact with the basioccipital. Occipital condyle below the level of the foramen magnum.

**DISCUSSION.** The right side of the skull is relatively intact whereas the left parietals and squamosals are broken. The skull is heavily impregnated with a dark mineral.

The CMP skull cannot be assigned to any known infraorder or genus. It is particularly unusual in the structure of the skull roof. The only other chelid that lack posterior and temporal emarginations on this scale is *Pseudemydura* in which the roof is extensive, the posterior emargination is replaced by a posterior dorsal extension of the supraoccipital, and the temporal emarginations are replaced by the extension of the squamosal. In the CMP skull, the supraoccipital forms relatively little of the skull roof and some posterior emargination is evident. The squamosal is expanded, as in *Pseudemydura*. As a consequence, the temporal roof is broad.

In *Pseudemydura*, expansion of the supraoccipital causes the hindmost portion of the skull to be lower than the parietals. In the CMP skull, the parietals extend back to the posterior margins of the skull and overlie most of the supraoccipital. This results in the skull having an anterior slope with its highest point behind the level of the quadrates.

The quadrates have an unusually deep ventral footing that forms a thick foundation for articulation with the lower jaw. The articulation facet is dislocated laterally and lies beneath the most lateral edge of the quadrate. These features, combined with the reduction of the alary process of the pterygoid indicate an unusual distribution of muscles between the upper and lower portions of the skull. The ventral portion of the cranium and the exoccipital regions are very similar to the arrangement found in all Cheloniinae.

#### PALAEOECOLOGY

Living Australian freshwater turtles have a variety of life history strategies and survival mechanisms (Kennett et al., 1993; Grigg et al., 1986; Georges, 1982; Georges et al., 1986; Georges & Kennett, 1989; Heaphy, 1990; Kennett & Georges, 1990; Georges, 1988; Thompson, 1988).

Several major trends which may have ecological significance are apparent in Oligocene-Miocene turtle assemblages at Riversleigh. Only 2 families, the Chelidae and Meiolaniidae are present and of these, chelids make up about 98% of material recovered. Chelids dominate these fossil assemblages in the same way that they dominate modern Australian freshwater systems (Legler, 1985). Only in a few, far northern localities are non-chelid freshwater turtles present; *Carettochelys insculpta*, the Pig Nose Turtle (a carettochelid), is found in a few NT rivers (Georges & Kennett, 1989; Heaphy, 1990). The earliest Chelids known are from the Cretaceous of Patagonia (de Broin, 1994) and the family is thought to have evolved in southern Gondwana (South America and Australia). A sister-group, the pelomedusids, evolved at the same time in northern Gondwana and fossils occur in Africa, Madagascar and South America.

Other turtles lived in Australia during the Oligocene-Miocene including the giant horned meiolaniids and soft-shelled trionychids (Gaffney, 1979, 1981).

Another feature of the Riversleigh fossil turtle fauna is the dominance of the plesiomorphic short-necked chelids. *Emydura/Elseya* turtles ac-

count for over 85% of turtle remains. Modern *Emydura/Elseya* are predominantly herbivorous and occur in coastal and inland rivers, creeks and lagoons, especially those with a well-developed aquatic flora (Cann, 1978; Legler, 1985). They are not abundant in muddy or stagnant water.

Chelids in System A are typically large with shells up to 500mm long and equivalent in size to the largest extant chelids. Chelid fossils from Systems B and C are smaller (shell lengths 200-300mm) and thinner-shelled. System C turtle is a dwarf with adult shell 100mm long. The large System A turtles occur at Site D (Archer et al., 1994) which yields many broken sections of unusually thick turtle shell. Carapacial plates 10-20mm thick are typical. From the larger shell pieces I estimate shell lengths of 350-450mm.

The largest extant chelids are the northern snapping turtle (*Elseya dentata*) and gulf snapping turtle (*Elseya lavarackorum*) which inhabit large flowing rivers or deep still water bodies (Cogger, 1992). The only other fossil chelids from Riversleigh that approach the dimensions of the System A turtles are late Pleistocene Terrace Site (White & Archer, 1994).

Species diversity increases from Systems A to C with 1 chelid species in System A, 2 chelids and 2 meiolanids in System B and 6 chelids and 1 meiolanid in System C. The increase in diversity suggests an increase in small, shallow or slow-flowing aquatic habitats from late Oligocene to middle Miocene.

Maximum turtle size is a useful indicator of water depth and flow rate. Riverine species that occur in deep or relatively fast-flowing water are typically large and capable of sustained swimming. Smaller species are excluded from such sites and often confined to fringe water bodies such as side-streams, overflows or ponds (Pritchard, 1979). The range of small-shelled chelids in System C sites suggests that a variety of shallow water or slow moving habitats were available at the time. System C turtles typically had shell lengths 150-250mm.

The smallest extant turtle is the bog turtle, *Clemmys muhlengergi*, an emydid (Pritchard, 1979) which is 76-114mm long. These turtles occur in extremely shallow, still water habitats; in some cases free water is not available. None of these sites are necessarily clear water sites (Behler & King, 1979).

In the Gregory River at Riversleigh there are 5 chelids; these, in order of abundance, are *Emydura* sp. aff. *subglobosa*, *Emydura* sp. aff. *victoriae*, *Elseya latisternum*, *Elseya lav-*

*arackorum* and *Chelodina rugosa*. The latter two are uncommon. This level of diversity is reasonably high for modern freshwater habitats in Australia. Species diversity increases as mean temperature and habitat variation increase (Obst, 1986).

Only Systems B and C contain large, terrestrial turtles (meiolaniids) with shell lengths up to 1 m long. Using *Meiolania platyceps* as a model, these creatures would have had average body masses of 150-200 kg.

There are a number of large, land turtles alive today. The best known are the various Galapagos tortoises (*Geochelone elephantopus*) and the Aldabran tortoise (*Geochelone gigantea*). Both reach body sizes and masses considerably greater than that calculated for Riversleigh's Miocene meiolaniids. They are regarded as examples of island endemism leading to gigantism (Pritchard, 1979). The majority of the extant large terrestrial turtles inhabit hot savanna regions of the world. For example, both species of large African land turtles (*Geochelone sulcata* and *G. pardalis*) occur in northern and central Africa. Neither species is found in dense forest. *G. sulcata*'s distribution is along the southern Sahara into central Africa (Pritchard, 1979). Savannah habitat verging onto treeless plains is the preferred habitat for all African land tortoises.

During the Miocene, Riversleigh was covered by wet forest communities (Archer et al., 1994) but the large land turtles seem incongruous in this habitat. Land turtles such as the South American *G. denticulata* and *G. carbonaria* are generalist herbivores and live in a range of habitats, including open savanna, closed woodland and rainforest (Bjorndal, 1989; Moskovits, 1985; Moskovits & Kiester, 1987). While both species will venture deep into rainforest and feed on fungi, fallen fruit and herbs, they do not permanently reside in the closed forest. Both prefer to reside near the forest-savanna interface (Moskovits & Bjorndal, 1990). Flowers and grasses form a major part of the diet of South American land turtles in savanna and swamp habitats. They consume sand which is thought to assist digestion of coarse fibrous matter; they are hind-gut fermenters and need a certain amount of fibre in their diet. In the rainforest, the turtles get fibrous foodstuffs in the form of vines and shoots, but these are usually not plentiful. In addition, the tortoises seek out clearings (e.g. sites of recent tree falls) to bask. Hind-gut digestion requires fairly high and constant temperatures (of 30° or more) and the turtles need to have periodic access to direct sunlight. Youn-

ger and smaller turtles need access to sunlight on a more regular basis than large adults (Moskovits, 1985).

If these limitations for giant land tortoises apply also to meiolaniid turtles living in or near forested habitats, then there must have been clearings where the animals could get sufficient volume of high fibre food and have direct access to sunlight. The rotund body form of these land turtles means that large animals would have a high thermal inertia. At air temperatures above 30° they may not need to seek additional external heat sources. However, should their body temperature fall below this level they would need to reach exposed sites quickly to restore core temperatures (Swingland & Frazier, 1979).

Riversleigh's meiolaniids are low in abundance despite their high diversity; 4 species in 2 genera are known from 5 individuals. Chelids, in contrast, are represented by hundreds of specimens. Nothing is known about dietary requirements of horned turtles. Large extant terrestrial turtles are opportunistic herbivores and have requirements for fibrous matter intake (Pritchard, 1976). The unusual structure of the jaws of meiolaniids indicates that some dietary selectivity may have been possible, but the nature of their diet is unknown.

The absence of soft-shelled trionychids from Riversleigh's Oligocene-Miocene coupled with the very low occurrence of long-necked turtles may be ecologically significant. Both types of turtles are 'ambush predators' (Pritchard, 1976). Both groups flourish in situations where they cannot be easily seen and this usually means turbid, muddy or dark water. Their absence and the preponderance of *Emydura/Elseya* suggests relatively clear water aquatic environments. *Chelodina* in System C coincides with the reduction in average chelid shell size, indicative of shallow, turbid lagoons during this period of the Miocene. The complete absence of trionychids suggests that the lagoons did not have silty bottoms and were unsuitable for concealment.

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